28. Note on the Skull of *Dinotherium giganteum* in the British Museum. By C. W. Andrews, D.Sc., F.R.S., F.Z.S.

(Submitted for Publication by permission of the Trustees of the British Museum.)

[Received March 5, 1921: Read May 24, 1921.]

(Text-figures 1–4.)

One of the most important specimens in the Geological Department of the British Museum is the fine skull of *Dinotherium giganteum*, which seems to be the only even approximately complete example at present known. The history of this specimen is of considerable interest. It was discovered in 1835 by Klipstein, about eighteen feet deep in the well-known ossiferous sands of Eppelsheim in Hesse-Darmstadt. An account of this discovery, including a description of the specimen and of the deposits in which it occurred, was published by Klipstein and Kaup in 1836 under the title "Beschreibung und Abbildungen von dem in Rheinhessen gefundenen colossalen Schädel des *Dinotherii gigantei*": in the following year a French translation of this paper appeared. Kaup, in his part of the memoir, not only gives a description of the skull itself, but also a very interesting account of the method of collecting the specimen. It appears that it was found lying on its dorsal surface in a bed of clay and sand. This was partly removed, leaving the skull resting on six pillars of matrix. Next, iron bars were passed through the openings thus made, which were then filled up with plaster of Paris. Next, the remaining portions of the matrix were removed and their place filled with more plaster, so that finally the skull rested on a solid base of plaster strengthened by iron bars. A stout board was inserted beneath the whole mass, which was then lifted from the excavation by twenty-four men with ropes. A quaint picture of this operation is given on the cover of Klipstein and Kaup's memoir. In this figure there is also shown a huge proboscidean femur, which is perhaps the original from which the cast of a Dinotherium femur now in the British Museum was made. In 1837 the skull was sent to be exhibited in Paris, part of the expenses of transport being borne by the French Academy. While there it was examined by de Blainville, whose description of the specimen is the best yet published; but even he was not allowed any opportunity of examining the dorsal surface. On the same occasion Isidore Geoffroy, Straus, and others took the opportunity of giving their views as to the structure and affinities of *Dinotherium*. It was then intended to send the specimen to London, but whether this was done on this occasion is uncertain. Some years later, in 1849, it was certainly in London, and was offered to the British

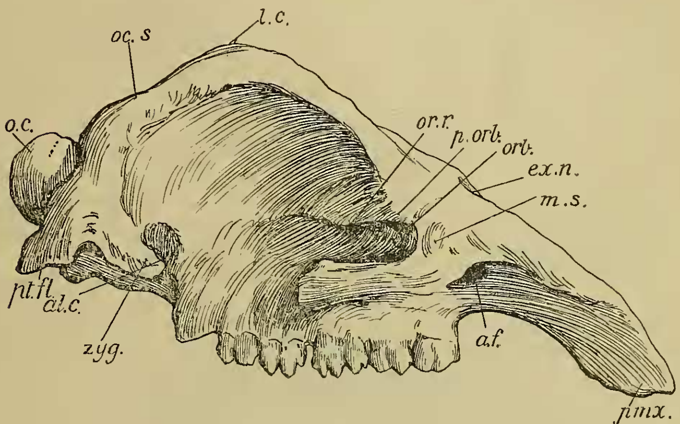
Museum for purchase ; it was then examined and reported on by Buckland and Owen. The purchase was not completed, and the skull seems to have been sent back to Darmstadt. About 1866, Klipstein sold his collection to Dr. Oldham, the Director of the Geological Survey of India, and from him the British Museum acquired not only this, but also some other valuable specimens, including the skull of *Dorcatherium nawi* and the front of the skull of *Tapirus priscus*.

Dr. W. D. Mathew, when visiting the Museum recently, pointed out to me that there is a widely-spread idea on the Continent that the skull now under discussion was broken up on its journey to London. This mistake has even appeared in print : thus Weinsheimer in his memoir on *Dinotherium* (Pal. Abhandl. Bd. i. 1883, p. 244), in speaking of the cast of this specimen, states that "The original of this cast no longer exists, since on its journey to London it was irretrievably broken into fragments." Examination of the skull shows that, in fact, at some time it has been much broken, but has been, on the whole, skilfully mended, the figures and cast no doubt having been followed in making the restoration.

In addition to Kaup's original descriptions and figures, de Blainville has given a very good account of the skull so far as he was able to examine it, and numerous other writers have referred to it. The most complete summary of the various views that have been held as to the affinities of *Dinotherium* is given by Stefanescu in his paper on *Dinotherium gigantissimum* (Anuarulu Museului de Geologia, etc., Bukarest, 1894, p. 126). It is now proposed to give a short description of the skull as it now is, followed by some discussion of the reasons for its peculiarities and of the relationships of *Dinotherium* to the other Proboscidea.

The occipital condyles (*o.c.*) are very large and prominent; ventrally and laterally they are limited by a deep groove, but dorsally they seem to pass uninterruptedly into the occipital surface (*oc.s.*). The articular surface of the condyles from above downwards makes rather more than a semicircle, so that the range of movement of the head up and down was extensive. Ventrally the condyles are separated by a broad, deep notch, in front of which the basioccipital runs downwards and forwards as a broad ridge, narrowing a little towards its junction with the basisphenoid, at which point, however, there is a prominence. The basisphenoid is not quite in the same straight line as the basioccipital, but seems to have been directed a little more upwards. The basis cranii as a whole slopes rather steeply downwards, making an angle of about 135 degrees with the plane of the teeth and the posterior part of the palate, which is regarded as being horizontal. From the outer angle of each condyle a ridge (*r.*) runs outwards and a little upwards, terminating in the outer angle of the squamosal (*a.s.*), which projects outwards far beyond the level of the zygomatic processes. These ridges, which towards their outer ends rise into thick and prominent crests, separate the upper occipital surface from the large post-tympanic flanges (*pt.fl.*), which appear to be formed partly by the exoccipitals and partly by the squamosal, though no suture can be seen; the angle between the post-tympanic flanges and the upper occipital surface is about 130 degrees. The ventral border of the flanges is gently convex, and is separated from the condyles on the inner side by a deep notch, which is partly occupied by a tongue-like process of bone, apparently the paroccipital process (*p.p.*) of the exoccipital. The anterior face of the flanges is concave from side to side, and is separated superiorly from the greatly elongated glenoid surface (*gl.*) for the mandible by a shallow transverse channel. Above

Text-figure 1.



Skull of *Dinotherium giganteum.*
From right side: about $\frac{1}{13}$ nat. size.

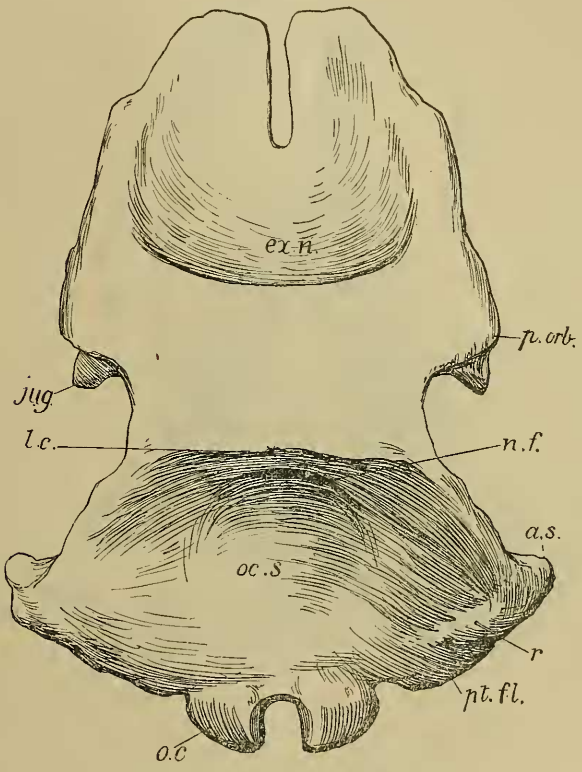
a.f., antorbital foramen; *al.c.*, posterior opening of alisphenoid canal; *ex.n.*, external nares; *l.c.*, lambdoidal crest; *m.s.*, depression for muscle attachment on preorbital prominence; *o.c.*, occipital condyle; *oc.s.*, occipital surface; *orb.*, orbit; *or.r.*, orbital ridge; *pmx.*, premaxilla; *p.orb.*, post-orbital process of frontal; *pt.fl.*, post-tympanic flange; *zyg.*, zygomatic process of squamosal.

the transverse ridges just described the occipital surface slopes forwards to a remarkable degree, giving the skull a curious resemblance, in this region, to the skull of some types of Whales. e. g. *Balænoptera.* The angle between the occipital surface and the basis cranii is about 53 degrees, so that the occiput is nearly parallel to the palatal surface. This extraordinary forward inclination of the occiput evidently limits the size of the cranial cavity, and de Blainville suggested that possibly the occipital surface had been crushed down towards the floor of the skull. Careful examination of the specimen, however, does not seem to support this idea, and it seems probable that, remarkable as the structure of this region of the skull may appear, it represents nearly the condition in the living animal. In other Proboscidea the occiput slopes strongly forwards, but this inclination is masked, in the adult at least, by the enormous development of cellular bone that takes place in this region, except over the area of the insertion of the ligamentum nuchæ, which occupies in consequence a deep depression.

In young individuals in which this development of the bone has not taken place, it can be seen that the occiput is inclined to the basis cranii at an angle about equal to that occurring in *Dinotherium*. Thus, in a figure of a median longitudinal section of the skull of a young African Elephant given by Flower ('Osteology of the Mammalia,' ed. 2, p. 181, fig. 59), the somewhat convex occipital surface is inclined to the basis cranii at an angle of about 40 degrees—that is, at a more acute angle than in *Dinotherium*. In the skulls of two very young Indian Elephants this angle was about 50 degrees, and in Palæomastodon, in which in the adult the spongy bone is relatively little developed, the angle is only about 35–40 degrees in the middle line. Thus it appears that the forward slope of the occiput relatively to the basis cranii is not really greater in *Dinotherium* than in the later Proboscidea, but only appears so because, when the palate and tooth series in *Dinotherium* is placed horizontally, the basis cranii slopes steeply downwards instead of being nearly horizontal.

In *Dinotherium* no development of cellular bone seems to have taken place, the necessary surface for the attachment of the muscles supporting the heavy head being in this case supplied by the great widening of the occipital surface, which is carried out laterally on to the lateral extensions of the squamosals (*a.s.*). The pit for the nuchal ligament (*n.l.*) is both wide and deep: behind it the occiput is convex from before backwards, while at the sides it is gently convex in all directions. Anteriorly the occiput is bounded by the transverse portion of the lambdoidal crest (*l.c.*), which is slightly convex forwards: in front of this the parieto-frontal surface makes an angle of about 140 degrees with the occiput. Laterally the lambdoidal crest reaches the upper border of the temporal fossa at about its middle point, and thence is continued downwards and backwards along its border to the lateral processes of the squamosal. The lateral portion of the occiput thus bounded, projects far over the enormous temporal fossa, forming a kind of roof to its posterior portion. The fronto-parietal region of the roof is short from before backwards and in its middle portion is flat or slightly concave. It first narrows a little, and then widens out and slopes down towards the post-orbital (*p.orb.*) processes, which are presumably borne by the frontals though no sutures are visible. A little in front of the level of the post-orbital processes the fronto-parietal region of the roof is bounded by a thickened border, which is concave forwards and forms the upper edge of the remarkably wide nasal opening (*ex.n.*). There is no trace of the nasal bones; they may have been lost, but in any case do not seem to have formed any median projection over the nasal opening. The maxilla (*mx.*), which formed the sides of the nasal opening at least in part, is a very massive and greatly developed bone. Externally to its tooth-bearing and palatal region it is produced laterally into a shelf of bone the hinder border of which is opposite the hinder lobe of the first molar. Posteriorly it forms the floor of the orbit, and no

Text-figure 2.

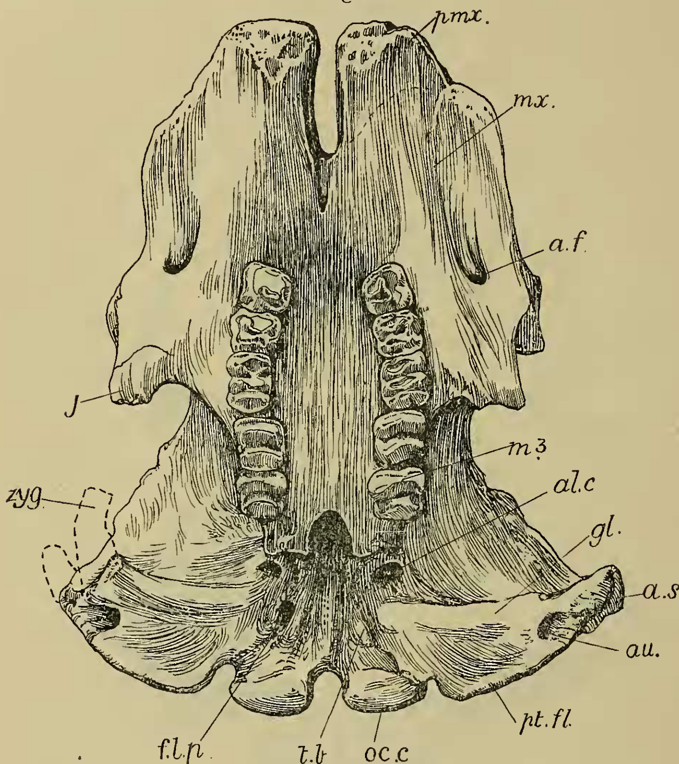


Skull of *Dinotherium giganteum.*
From above: about $\frac{1}{13}$ nat. size.

a.s., outer angle of squamosal; *ex.n.*, external nares; *jug.*, jugal; *l.c.*, lambdoidal crest; *n.f.*, nuchal fossa: *o.c.*, occipital condyles; *oc.s.*, occipital surface; *p.orb.*, postorbital process of frontal; *pt.fl.*, post-tympanic flange; *r.*, ridge from outer angle of squamosal.

doubt joined the jugal, on which the lower post-orbital process is borne. In front of the orbit the maxilla forms a great mass of bone, terminating laterally in a rugose somewhat concave surface for the attachment of a muscle (*m.s.*), probably the maxillolabialis superior. The lachrymal bone perhaps took part in the formation of this pre-orbital mass, but its limits cannot be determined. The very large antorbital foramen (*a.f.*) opens on the lower surface of the maxilla, about mid-way between its prominent pre-orbital boss and the premolar teeth. The point of union of the maxillæ with the premaxillæ is probably marked by

Text-figure 3.



Skull of *Dinotherium giganteum.*
From below: about $\frac{1}{13}$ nat. size.

a.f., antorbital foramen; *al.c.*, posterior opening of alisphenoid canal; *a.s.*, outer angle of squamosal; *au.*, external auditory meatus; *f.l.p.*, ? foramen lacerum posterius; *j.*, jugal; *gl.*, glenoid surface for mandible; *m.* 3, third molar; *mx.*, maxilla: *oc.c.*, occipital condyles; *pmx.*, premaxilla; *pt.fl.*, post-tympanic flange; *t.b.*, ? tympanic bulla; *zyg.*, zygomatic process of the squamosal.

the sudden narrowing of the snout about 40 centimetres in front of the orbit. The suture between the two bones can be traced for a short distance on the palatal surface.

The premaxillæ (*pmx.*), though narrower than the maxillæ, are still very massive and widely expanded. Their upper surface is concave from side to side, the lower convex in the same direction. In the mid-ventral line they are separated in the actual skull by a cleft, probably the result of distortion through crushing: in the cast, which seems to have been made before the skull had been broken, there is only a deep groove. From the posterior angles of this groove a pair of ridges run back on the palatal surface to the anterior end of the tooth series.

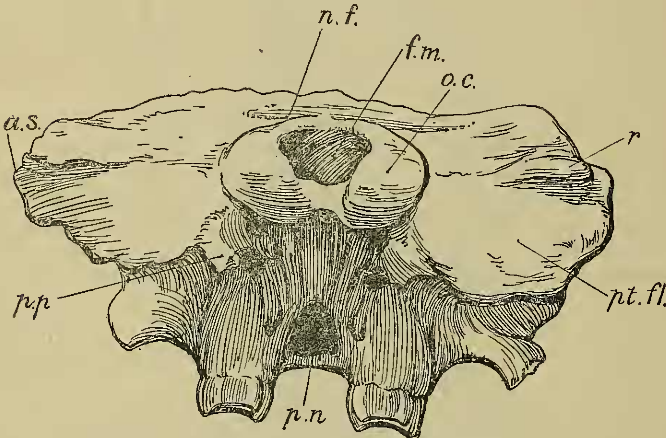
The anterior ends of the premaxillæ are thickened, and terminate in a nearly flat surface in which there are some irregular asymmetrically arranged pits but no real trace of any incisor alveoli, though it seems not unlikely that incisors will be found to have been present in the young animal. The anterior portion of the skull in front of the tooth series is curved downwards, its palatal surface approximately following the curve of the downturned mandibular symphysis.

The structure of the basal region of the skull is not very clear, probably in consequence of the crushing and fracturing it has undergone. On either side of the basioccipital there is a fairly well-developed auditory bulla (*t.b.*). External to this is a strong crest of bone, terminating posteriorly at the process described above as the paroccipital (*p.p.*). Anteriorly it runs inwards to the sides of the basisphenoid. This crest, which seems—at least in front—to be formed by the pterygoid, turns downwards anteriorly, and forms the border of the narrow opening of the posterior nares (*p.n.*): ventrally it terminates just behind the tooth series in a boss of bone which forms the posterior angle of the hard palate. Dorsal to this boss there is a deep fossa, presumably in the palatine, passing upwards to the hinder opening of the alisphenoid canal (*al.c.*). Behind and a little to the outer side of this opening is the inner end of the extraordinarily elongated glenoid surface (*gl.*) for the mandible. This surface is very narrow from before backwards and gently convex in the same direction: posteriorly it is bounded by the depression separating it from the post-tympanic flange. Its outer end is immediately behind the base of the zygomatic process (*zyg.*) of the squamosal, and its anterior border, at least in its outer half, abuts on the temporal fossa. The auditory opening (*au.o.*) is opposite the outer border of the zygomatic process: the external auditory meatus is greatly elongated, and its floor is formed by the roof of the channel behind the glenoid surface. Above the auditory opening the massive lateral angle of the squamosal (*a.s.*) projects outwards some fourteen or fifteen centimetres. The structure of a bony labyrinth supposed to belong to *Dinotherium* has been described and figured by Claudius ("Das Gehorlabyrinth von *Dinotherium giganteum*," Palæontographica, vol. xiii. (1864–66) p. 65).

The opening of the optic foramen is indicated by a depression, from the upper edge of which a downwardly deflected ridge (*or.r.*) runs upwards and forwards across the side wall of the skull and terminates in front in the post-orbital process (*p.orb.*). Towards its anterior end it becomes very prominent, sharply delimiting the eye-socket above. This ridge seems to be very characteristic of the Proboscidea: it occurs in *Mœritherium* and probably in all the members of the group.

The skull of *Dinotherium* is, in many respects, one of the most remarkable known. Although fundamentally its characters are clearly Proboscidean, nevertheless it differs widely from the skulls of the other members of the group and, indeed, in some respects from that of any other mammal. In the true Elephants and

Text-figure 4.



Skull of *Dinotherium giganteum*.
From behind: about $\frac{1}{13}$ nat. size.

a.s., outer angle of squamosal; *f.m.*, foramen magnum; *n.f.*, nuchal fossa; *o.c.*, occipital condyle; *p.n.*, posterior nares; *p.p.*, paroccipital process; *pt.fl.*, post-tympanic flange; *r.*, ridge from outer angle of squamosal.

Mastodons the peculiar form of the skull is mainly due to the enormous development of cellular bone in the occipital region, increasing the area available for the attachment of the muscles necessary for the support of the heavy trunk and tusks. In *Dinotherium*, although the upper tusks are wanting, the trunk, judging from the large size of the nasal opening, must have been enormous, and the weight of the head was further increased by the great deflected mandibular symphysis with its large tusks. In this case, however, the area for the attachment of the supporting muscles was supplied by the widening out of the occipital surface, which was further increased laterally by the extension outwards of the squamosals. Little or no cellular bone seems to have been developed, the occipital surface above the post-tympanic flanges being nearly flat except for the depression for the nuchal ligament. This flattening of the occiput, combined with its forward inclination, must have made it possible for the animal to move its head up and down through a large arc, a movement perhaps connected with the use of the downwardly directed lower tusks. The great width of the proboscis, probably rendered possible by the absence of upper tusks, led to the widening out of the skull in the orbital region, producing the shelf-like projection of the maxillæ above noticed. The great width of the glenoid surface for the mandible is a peculiarity for which it is difficult to account, unless it is correlated with the general widening of this region of the skull.

The skeleton of *Dinotherium* is still very imperfectly known, but such bones as have been described show that the animal must have been quite Elephantine in structure and appearance except as to its head, the legs being pillar-like and the neck short. A femur probably associated with the skull above described measured 150 cm. in length. The numerous speculations as to the appearance and habits of *Dinotherium* have been summarized by de Blainville and Stefanescu in their works referred to above. Most writers seem to suppose that the animal was chiefly fluviatile and aquatic in its habits, but there appears to be no good reason for believing that it was more so than the Elephants.

The origin of *Dinotherium* is a question of much obscurity. The genus must have branched off from the main Proboscidean stem at a very early date, probably originating from an animal in much the same stage of evolution as *Mœritherium*, the teeth being still simply bilophodont. The premolar series is more highly modified than in *Mœritherium*, the series being reduced to pm. 3 and pm. 4, the latter being bilophodont like the posterior molars. This modification of the premolars, like the acquisition of the third ridge in m. 1 and the reduction of the heel of m. 3, may have arisen after the divergence from the main stock had taken place. It is interesting to note that the last lower milk molar of *Mœritherium* shows a strong tendency to trilophodonty, the posterior ridge being fairly distinct: in *Dinotherium* also this tooth is trilophodont. If, as seems almost certain, *Dinotherium* originated from some small comparatively generalized type, it is interesting to note how, after its separation from the main stock, the direction of evolution is almost the same as in the latter. Thus there was a general increase in stature, which, being accompanied by a shortening of the neck, necessitated, as in the Elephants and Mastodons, the development of an elongated snout; so that it may be regarded as certain that *Dinotherium* passed through a longirostrine stage comparable to that of which the beginning is seen in *Palæomastodon* and the culmination, so far as the elongation of the lower jaw is concerned, in *Tetrabelodon angustidens*. Subsequently the symphysis became somewhat shortened and was deflected, the lower incisors at the same time becoming enlarged. It is interesting to notice that a tendency to a similar type of modification of the mandible occurs in that group of Tetrabelodonts to which Professor Osborn gives the name Rhynchorostrinæ, the most extreme case being *T. dinotherioides*. This deflexion of the mandibular symphysis led to the development of the flexible free trunk, just as the shortening of the symphysis did in the main stem, but while in this the upper incisors tended to increase in size, in the Dinotheres they disappeared.

The dimensions of the skull above described (taken on the cast) are :—

	cm.
Length from occipital condyle to tip of premaxillæ.	121
Length from posterior border of palate to tip of premaxillæ	84
Width between outer angles of the squamosals ...	90
Width between outer borders of the zygomatic processes	74
Width between the openings of the ear	68
Length of glenoid surface from before backwards.	6·3
Width of glenoid surface from side to side	24
Width of the occipital condyles	31
Width of skull just in front of the ant-orbital foramen	57
Width of the anterior end of the premaxillæ	31
Length of molar-premolar series	47
Length of molar series	30·2